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Responses of field-grown soybean (cv. Essex) to elevated SO_2 under two atmospheric CO_2 concentrations

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Abstract

The objective of this research was to determine the effects of elevated concentrations of carbon dioxide (CO_2) and sulfur dioxide (SO_2) on field-grown soybean. Soybeans (*Glycine max L. Merr. cv. 'Essex'*) were grown a full-season in open-top field chambers exposed to either ambient (350 $\mu l\ L^{-1}$) or elevated CO_2 (500 $\mu l\ L^{-1}$) levels under two levels of SO_2 (0.00 and 0.12 $\mu l\ L^{-1}$). Enriched CO_2, with or without SO_2 treatments, significantly increased net photosynthesis rates, leaf area index (LAI; in R4 growth stage) and leaf dry weight, but did not significantly affect stomatal resistance, transpiration rates, leaf area, plant height, total biomass or grain yield. Elevated SO_2 treatments significantly decreased photosynthesis and LAI during pod fill stages, but did not significantly affect stomatal resistance, transpiration, total biomass, plant height or grain yield. Sulfur dioxide inhibited growth and development (i.e., LAI) during canopy coverage before any effects on photosynthesis were detected. The interactive effects of CO_2 and SO_2 treatments on the gas exchange parameters were significant during pod fill, where high SO_2 reduced photosynthesis at ambient CO_2 but not under elevated CO_2. Leaf area index values were likewise reduced by SO_2 exposure under ambient CO_2 during late flowering and pod fill stages. Thus, enriched CO_2 under high SO_2 exposure partially compensated for the negative impact of SO_2 stress on PS and LAI during the pod fill stages. © 1997 Elsevier Science B.V.

Key words: Soybean (*Glycine max* L.); SO_2; CO_2; Biomass; Climate changes; Grain yield; Photosynthesis; Plant growth

1. Introduction

Global carbon dioxide (CO_2) concentrations have increased from about 290 $\mu l\ L^{-1}$ in the late 1800's to current levels of around 350 $\mu l\ L^{-1}$ [6, 15]. Atmospheric CO_2 concentrations are currently increasing by about 1% annually. Projected increases are for a doubling of CO_2 concentration within the next century [6, 10, 17].

It is well recognized that atmospheric CO_2 enrichment has a positive physiological impact on plants [7, 21, 30]. Several studies using controlled environment chambers have shown that CO_2 may compensate for sulfur dioxide (SO_2)-induced leaf injury [3, 8, 11, 26, 28, 34, 38]. However, only a few field studies involving interactions of CO_2 enrichment

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and stress induced by SO_2 have been reported [32, 34]. The responses of plants to the 'greenhouse' environment, i.e. the simultaneous effects of elevated CO_2 and increased air pollution are not well recognized, although such information is essential for a proper prognosis of the impacts of climate changes on agriculture [1].

Previous reports on physiological and yield results from CO_2 and O_3 interaction investigations using open-top chambers (OTCs) on crop plants (e.g. soybean, wheat, corn and cotton) suggest that increasing the atmospheric CO_2 concentration to 500 $\mu l\ L^{-1}$ partially overcame O_3-induced reductions of photosynthesis (PS) and yield loss caused by current ambient levels [4, 31, 32]. The objective of the current study was to determine the interactive effects of CO_2 enrichment on chronic low-level SO_2 stress concerning physiological responses of soybean cv. 'Essex' in the field. Specific objectives were to determine the combined effects of these gases on leaf characteristics such as leaf gas exchange, leaf area index (LAI), plant height and growth, and grain yields, and to test the hypothesis that elevated CO_2 ameliorates the detrimental effects of SO_2 stress by altering the physiology of the plant.

2. Materials and methods

Field studies using OTCs were conducted during the summer months of 1991 at the USDA Beltsville Agricultural Research Center, South Farm, Beltsville, Maryland.

Soybean (*Glycine max. L. Merr. cv. 'Essex'*) seeds were planted in 4 m × 5 m plots in rows 0.5 m apart on 4 June 1991. Shortly after emergence, with primary leaves unfolded, seedlings were thinned to approximately 0.1 m within rows (between-plant distance). This produced a stand density of approximately 20 plants m^{-2} (200 000 plants ha^{-1}) for each chamber.

Cultural practices and OTCs were described earlier [13, 18, 24]. Once plant stands were established (V1; i.e. fully developed leaves at unifoliolate nodes), OTCs (3 m in diameter and 2.5 m in height) were placed over the plot areas on 21 June. Treatments were started on 2 July. All OTCs had blowers equipped with carbon-filters (CF) and particulate filters. The chambers were supplied about three changes of air per minute. The blowers were in operation 24 hr day^{-1} until senescence of plants in late October.

The study examined the effects of 500 $\mu l\ L^{-1}$ CO_2 (the CO_2 concentration projected for the mid-twenty first century) [6] in combination with SO_2 at 0.12 $\mu l\ L^{-1}$ (potentially toxic effects over long term exposure) [14]. The experimental design was a 2 × 2 factorial of CO_2 and SO_2 treatments arranged in a randomized complete block design [12].

The following SO_2 and CO_2 treatments were used: (1) low-SO_2 (CF air) and ambient-CO_2(350 $\mu l\ L^{-1}$); (2) high-SO_2 (CF + 0.12 $\mu l\ L^{-1}$ SO_2) and ambient-CO_2; (3) low-SO_2 (CF air) and enriched CO_2 [CF air + 150 $\mu l\ L^{-1}$ CO_2 (500 $\mu l\ L^{-1}$)]; and (4) high-SO_2 (CF + 0.12 $\mu l\ L^{-1}$ SO_2) and enriched CO_2 (CF air + 150 $\mu l\ L^{-1}$ CO_2). All treatments were replicated three times; hence, twelve OTCs were used. The elevated CO_2 treatments were applied 12 hr day^{-1} (0600 to 1800 EST) 7 day wk^{-1}, for a total of 82 days. The elevated SO_2 treatments were applied 5 hr day^{-1} (1000 to 1500 EST), 5 day wk^{-1}, for a total of 56 days. The SO_2 was added Monday through Friday, except on days with rain (4 days). The CO_2 and/or SO_2 treatments were supplied as cylinder gases (C.P. grade, 99.8%) purchased from commercial sources (Air Products, Inc., Allentown, PA). The flow rates for each chamber treatment were regulated by flow meters and were adjusted daily. Treatment gases were delivered to each chamber via separate Teflon^R tubes (6.4 mm O.D.) for each gas and injected into the blower that mixed the gases with CF air prior to entering the chambers. Teflon^R air sample lines were placed in the center of each chamber near the top of the plant canopy to monitor the treatment SO_2 and CO_2 levels on an hourly basis during the injection periods. A solenoid-valve switching system was used to alternately monitor air samples from each chamber. Chamber CO_2 concentrations were measured using an infrared gas analyzer (Model No. LIRA MSA 3200, Mine Safety Co., Pittsburgh, PA). The SO_2 concentrations were measured using a pulsed fluorescence SO_2 analyzer [Model No.43, Thermo Electron Corp (TECO), Franklin, MA]. A TECO Model 143 SO_2 permeation tube calibrator system

was used to calibrate the SO_2 analyzer at least once a week. The Maryland State Environmental Agency audited the SO_2 monitors at the field site, ensuring that they met EPA accuracy and performance standards.

The chamber air treatments were terminated when plants reached growth stage R8 (i.e. 95% of the pods reached their mature pod color). The blowers operated until seed harvest to facilitate drying.

Net photosynthesis (PS) and stomatal resistance (RS) rates were measured using a model NO. LI-6200 portable PS system (LI-COR, Inc., Lincoln, NE). Details on gas exchange measurement techniques were described previously [24, 32]. Measurements were made on cloud-free days near the solar zenith. Three randomly selected plants per chamber were examined. PS and RS determinations were made on middle leaflets of fully expanded trifoliates located on the third or fourth node of the main stem below the apex. Gas exchange data were collected at several growth stages (V5, Rl, R2, R4, R5, R6) on a weekly or biweekly basis.

Effects of treatments on growth were determined by measurement of accumulated biomass of various organs, leaf area index, and plant heights. Accumulated biomass was determined on plants harvested during the latter phase of pod fill (R6 stage). To eliminate 'edge-effects' in the chamber, 10 plants from the four center rows per replicate treatment were harvested, i.e. cut at the hypocotyl, from which the following organs were harvested: leaves, stems, and pods. Data were collected on site for pod number, fresh weight and leaf area. Leaf areas were determined using a leaf area meter (Model No. LI-3100; LI-COR Inc., Lincoln, NE). All organ samples were oven-dried for 48 hr at 70°C and weighed.

Non-destructive leaf area index (LAI) values were measured on several dates throughout the season using a plant canopy analyzer (Model No. LAI-2000, LI-COR, Inc., Lincoln, NE). The instrument computed LAI from measurements of the incoming solar diffuse radiation, above and below the canopy, at five different angles simultaneously. Duplicate measurements were taken from each chamber treatment, with each measurement being a mean of four individual readings sequentially taken at ground level from the base of one row to an adjacent row having a 45° degree angle path.

Plant heights were determined at four growth stages (V7, V10, V11, and R2). Measurements were taken from the cotyledonary node to the uppermost node with a fully developed leaf on the main stem. Three plants per chamber were selected at random on each date; thus, each mean represents the average of 9 plants per treatment. Grain yields at maturity were determined by harvesting 40 comparable plants from each chamber and threshing on-site using a small-plot thresher. The air-dry grain samples were weighed for yield determination. Seed weights per 100 seeds were estimated by determining the weights of 1000 seeds and dividing by 10.

Data were analyzed using SAS procedures for individual dates and combined over time. Analysis of variance (ANOVA) was carried out using the average values per replicate treatment; these data were used by SAS to test main and interactive effects. Main effect means and interactive effect means were separated using least significant difference (LSD) comparisons when ANOVA's F-tests were significant ($P<0.05$).

3. Results

3.1. Air quality, environmental conditions and foliar injury

General environmental conditions at USDA-BARC during May through August 1991 and the longer-term averages (1970–1990) are summarized in Table 1. Total rainfall amounts for May through August 1991 were 33% of the longer-term averages at Beltsville, Maryland. Monthly air temperatures May through August, 1991 were approximately 2°C above the longer term values. Ambient air in Maryland during 1991 summer months had mean O_3 concentrations for 10 hr (0800–1800 hr) that averaged 0.06 ± 0.005 $\mu l\ L^{-1}$ O_3 [31, 32]. In 1991, the average ambient concentration of SO_2 during the summer months was 0.006 $\mu l\ L^{-1}$. This values is below the established air quality standard (0.03 $\mu l\ L^{-1}$ SO_2).

The high moisture holding capacity of the

Table 1
Summary of total precipitation, means of daily temperature and solar radiation levels at USDA-BARC from May through August for 1991 and longer-term exposure (1970 to 1990)

	May	June	July	August	Avg. June–August
Precipitation (cm)	1.7	4.1	3.8	2.6	12.2
†Longer-term avg.	9.7	9.9	10.5	12.0	42.1
Air Temperature (°C)	20.9	22.8	25.2	24.4	23.3
†Longer-term avg.	16.6	21.3	24.0	23.3	21.3
Solar Radiation (MJ m^{-2})	668	621	566	574	607

†Average (1970–1990): data obtained from Climatology of Maryland and Delaware, Department of Commerce, NOAA, Vol. 96, 1992.

Cordors silt loam soil provided near adequate moisture levels for normal growth of the plants even though precipitation amounts and frequency were substantially below the longer-term amounts for the region. Supplemental irrigations approximately 2.5 cm each were provided on several occasions to prevent problems with moisture stress; however, general symptoms of moisture stress were typically absent within the plant canopy at all times. The irrigations were normally applied late in the afternoons following terminations of the daily SO_2 treatment to avoid problems with SO_2 forming H_2SO_4 on the wet foliage.

Evidence of SO_2 injury to foliage in the high SO_2 treatment chambers was present on a single occasion in mid-July. The SO_2-induced leaf injury was largely absent during August as the plants matured. The upper leaves in the canopy were typically free of symptoms within two weeks as new leaves appeared above the site of SO_2 injury as described by Rudorff et al. [32].

3.2. Leaf photosynthesis

Comparisons of main effect means for CO_2 and SO_2 and their interactions within the growing season for photosynthesis (PS), stomatal resistance (RS) and transpiration (TR) at vegetative and flowering to pod filling stages are shown in Table 2. Means were combined over three dates during the vegetative/flowering stages (i.e. V5, R1, and R2) and three dates during reproductive stages (i.e. R4, R5, and R6) during pod fill. Plants treated with elevated CO_2 consistently exhibited significantly increased net PS rates throughout the growing season, averaging 25.1% above those for the CF control in the absence of SO_2, and 33.4 % in the presence of SO_2. This CO_2 stimulation of PS was observed in all stages. Photosynthetic response to elevated SO_2 was non-significant ($P>0.05$) during pre-pod fill stages; however, combined over dates during pod fill stages, the PS rate for the CF + SO_2 treatment averaged 17.2%, lower than that for CF air alone, which was significant at the 5% level. When combined over three dates during pod fill, the PS rates showed interactive effects with SO_2 exposures (Table 2). During pod fill, the negative impacts of SO_2 stress on PS were significant ($P<0.05$) at ambient CO_2, but insignificant ($P>0.05$) in the high CO_2 treatment.

3.3. Growth, biomass and grain yield responses

Leaf area index (LAI) values were determined using a non-destructive method (Table 3). Data presented on LAI for 4 measurement dates (V6, R1, R4 and R6) were normalized to the carbon filtered (350 $\mu l\ L^{-1}$ CO_2) with no SO_2 added. Elevated CO_2 alone significantly increased LAI values at growth stages R1, R4, and R6. Elevated SO_2 alone significantly decreased LAI at growth stages R1 and R4. Elevated CO_2, combined with elevated SO_2 significantly decreased the detrimental effect of SO_2 alone by increasing LAI at growth stages V6, R1 and R4. Elevated CO_2 significantly increased LAI about 3% at low SO_2 and by 5–10% at elevated SO_2.

Leaf area, leaf dry weights (DW), plant heights (at R2 stage), total plant dry biomass (leaf, stem and pod) and grain yield results are shown in Table

Table 2
Effects of CO_2 and SO_2 treatments on net photosynthesis (PS, μmol m^{-2} s^{-1}), stomatal resistance (RS, s cm^{-1}), and transpiration (TR, μmol m^{-2} s^{-1}) at vegetative and flowering to pod filling stages

Treatments		†Late Vegetative-Flowering			‡Pod Fill		
CO_2	SO_2	PS	RS	TR	PS	RS	TR
				CO_2 Means Combined Over SO_2 Treatments			
350 μl L^{-1} CO_2		23.2 b*	0.221	5.23	21.5 b	0.507	2.94
500 μl L^{-1} CO_2		29.2 a	0.234	4.95	28.6 a	0.520	2.71
				§SO_2 Means Combined Over CO_2			
350 μl L^{-1} CO_2		26.0	0.226	5.35	26.2 a	0.462	3.06
350 μl L^{-1} CO_2	SO_2	26.3	0.229	4.83	23.7 b	0.565	2.59
				CO_2 and SO_2 Interaction Means			
350 μl L^{-1} CO_2	CF (i.e. low SO_2)	23.0 b	0.209	5.59	23.3 b	0.427	3.10
350 μl L^{-1} CO_2	CF + high SO_2§	23.3 b	0.233	4.87	19.7 c	0.586	2.77
500 μl L^{-1} CO_2	CF (i.e. low SO_2)	28.9 a	0.242	5.10	29.0 a	0.496	3.02
500 μl L^{-1} CO_2	CF + high SO_2	29.4 a	0.225	4.80	27.7 a	0.543	2.40

*Means followed by the same letters within a column are not significantly different at $P<0.05$.
†The late vegetative-flowering represented measurements at V5, R1, and R2 ($n=18$) growth stages.
‡Pod fill represented measurements at R4, R5, and R6 ($n=18$) growth stages.
§SO_2 treatments were at 0.12 μl L^{-1} for 5 hr day^{-1} 5 days a week. CF = charcoal filtered air.

Table 3
Relative effects of CO_2 and SO_2 treatments on LAI normalized to the charcoal-filtered air chambers with no SO_2 added for 4 measurements during vegetative-flowering and pod fill stages.

Treatment	Day 207	Day 210	Day 219	Day 226
		Stage of Development		
	(V6)	(R1)	(R4)	(R6)
		% of Control		
		CO_2 Treatment Means		
350 μl $L^{-1}CO_2$	97	95 a*	98 a	102 a
500 μl $L^{-1}CO_2$	102	101 b	103 b	116 b
		‡SO_2 Treatment Means		
CF	102	100 b	102 b	108 a
CF + SO_2	98	94 a	99 a	110 a
		CO_2 and ‡SO_2 Interaction Means		
350 μl L^{-1} CO_2CF	†100 ab	†100 b	†100 b	†100
350 μl L^{-1} CO_2CF + SO_2	95 a	90 a	96 a	102
500 μl L^{-1} CO_2CF	103 ab	101 b	104 c	115
500 μl $L^{-1}CO_2$CF + SO_2	101 b	100 b	102 b	118

*Within a column, values having a letter in common are not significantly different at $p<0.05$.
†100% values were 4.6. 5.9, 7.1, and 6.0 m^2 leaf/m^2 soil for days 207, 210, and 226, respectively.
‡SO_2 treatments were at 0.12 μl L^{-1} for 5 hr day^{-1}, 5 days a week. CF = charcoal filtered air.

Table 4
Effects of CO_2 and SO_2 treatments on plant growth, biomass, and grain yields.

Treatment	Leaf Area dm^2/plant	Leaf DW g/plant	Height cm	*Total Biomass g/plant	Seed Wt % of control	100 Seed Wt g
			CO_2 Treatment Means			
350 $\mu l\ L^{-1} CO_2$	28.9	18.4 b*	101	49.0	89.9	13.9
500 $\mu l\ L^{-1} CO_2$	29.9	22.2 a	98	55.6	100.3	14.0
			‡SO_2 Treatment Means			
CF	30.9	21.5	99	56.1	97.7	14.2
CF + SO_2	28.0	19.0	101	48.6	92.1	13.7
			CO_2 and ‡SO_2 Treatment Means			
350 $\mu l\ L^{-1}$ CO_2CF	29.3	18.9 b	100	49.7	†100.0	14.5
350 $\mu l\ L^{-1}$ CO_2CF + SO_2	28.4	17.9 b	102	48.3	79.4	13.2
500 $\mu l\ L^{-1}$ CO_2CF	33.4	25.3 a	97	65.8	95.5	13.8
500 $\mu l\ L^{-1}$ CO_2CF + SO_2	27.6	20.2 b	100	48.9	105.1	14.2

*Within a column, values having a letter in common are not significantly different at $p < 0.05$.
*Dry weight of seeds, pods, stems, and leaves at pod maturity.
†Charcoal filtered air chambers = Control, 31.6 g/plant.
‡SO_2 treatments were at 0.12 $\mu l\ L^{-1}$ for 5 hr day^{-1}, 5 days a week.

4. Plants treated with elevated CO_2 exhibited significantly increased leaf DW in the absence of SO_2 exposure, averaging 34% above that of the CF control, but leaf DW was not significantly increased (i.e. only 7%) in the presence of SO_2. Elevated SO_2 alone did not significantly affect leaf DW. Leaf DW for the CF + SO_2 treatment averaged 5.3% below that for CF air alone (Table 4). Leaf dry weight (DW) values were significantly increased in the elevated CO_2 plots. Plant heights (at R4 stage) appeared unaffected by treatments; however, leaf area and total plant biomass exhibited trends for higher values under elevated CO_2 alone which is consistent with the LAI data.

Seed yields presented as % of control with the ambient CO_2 and low SO_2 treatment set at 100 (Table 4) showed that elevated CO_2 failed to produce significant gains in grain yield. Plants in the CF + CO_2 treatments alone experienced some lodging during early pod fill which likely contributed to variation in the biomass and grain yield results. No significant CO_2 or SO_2 effects were observed regarding seed yield. Also, there were no interactive effects of CO_2 and SO_2 treatments on seed yields.

In the present study, SO_2 at 0.12 $\mu l\ L^{-1}$ showed only a tendency to reduce biomass and grain yields. Except for PS, LAI and leaf DW, the interactive effects of $CO_2 \times SO_2$ on growth and physiological responses were generally non-significant. SO_2 fumigations in July, during that vegetative stage, affected LAI but not PS.

4. Discussion

Increasing concentrations of CO_2 in the atmosphere are known to increase the rate of PS and to reduce photorespiration in most plants, especially C_3 plants [30, 39] while SO_2 exposure is known to reduce net PS [11, 20, 35]. The literature also reveals that chronic SO_2 exposures may either inhibit or stimulate gas exchange, depending on exposure dose and species involved [5, 37]. Such diverse reports indicate that it is very difficult to make generalizations about the effects of SO_2 on gas exchange processes. Muller et al. [25] exposed field-grown soybean (cv. Wells) to 24 fumigations throughout the season with 0.117 $\mu l\ L^{-1}$ SO_2 treatments, finding results similar to ours, i.e. 0.117 $\mu l\ L^{-1}$ SO_2 treatments did not reduce PS. Carlson and Bazzaz [9] showed that elevated CO_2 reduced the sensitivity of various plant species to SO_2 damage. As in a previous study [24] the current study showed that elevated CO_2 enrichment stimulated PS rates.

Similar results in terms of a counteracting effect of CO_2 against SO_2 stress on PS were also observed in soybean (cv. William) by Sandhu et al. [34] and in *Chlorophytum comosum* [26]. High PS rates observed under enriched-CO_2 were possibly the result of reduced photorespiration [19]. Black [3] suggested that protection against SO_2 may be owing to stomatal closure as CO_2 is increased, but other internal factors owing to enhanced PS could also offer enhanced resistance through metabolic use of SO_2 or repair of damage that might be cause by SO_2 [1]. Rao and De Kok [28] reported that combined exposure of wheat (cv. Urban) to high CO_2 (700 μl L^{-1}) prevented negative effects of high SO_2 (0.14 μl L^{-1}). A significant increase in ascorbate and glutathione levels and in their redox states was observed in plants exposed to high CO_2 and SO_2, compared with plants exposed to SO_2 alone [28]. Kropff [16] measured the effect of SO_2 (<0.1 μl L^{-1}) on PS at different CO_2 concentrations while analyzing the contribution of stomatal and non-stomatal factors to PS inhibition. Stomatal resistance was not directly affected by SO_2 fumigation, but was indirectly attached as a result of a feedback loop between net PS and internal CO_2 concentration.

Our data showed that combined over three dates, both during pre-pod fill and pod fill stages, RS and TR were not significantly affected by the CO_2 enrichment treatments (Table 2). We expected that increasing the CO_2 concentration by 150 μl L^{-1} would cause increased RS and decreased TR rates (e.g. Mulchi et al. [24]), but Table 2 shows that the effects were minimal and non-significant. However, water-use-efficiency was likely increased in plants receiving elevated CO_2 both in the presence and absence of SO_2 (e.g. Sage and Reid [33]). Considering that the RS and TR values (Table 2) were not significantly affected by the SO_2 exposure, we suggest that the results are consistent with the ability of the 'Essex' soybean cultivar to metabolize phytotoxic sulfite to the less toxic sulfate, as suggested by Miller and Xerikos [23] rather than by excluding it from leaves.

Stomata are known to play an important role in mediating the response of plants to air pollutants by affecting SO_2 uptake (e.g. Rennenberg and Polle [29]). However, stomatal responses to SO_2 are very complex. The effect of SO_2 depends on such factors as air humidity, light intensity, physiological activity of tissue, and pH value inside plant cells (e.g. Niewiadomska and Miszalski [26]). There is no simple pattern of stomatal response to SO_2, and many of the apparent inconsistencies in results on gas exchange may be explained by the complexity of SO_2/stomatal interrelationships, in which stomatal responses are modified by many factors ([e.g. Black [4]). Niewiadomoska and Miszalaski [26] suggested that the CO_2 protecting effect against SO_2 does not depend on the rate of SO_2 penetration into the leaf. Spedding [36] suggested that humidity influenced the assimilation of SO_2 when the stomata were closed and that the gas entered the plant tissues through the cuticle.

Effects of CO_2 and SO_2 on total chlorophyll concentration (CHL), specific leaf weight (SLW) and photochemical efficiency (F_v/F_m) in soybean (cv. Essex) were reported earlier [32]. Those data showed that F_v/F_m was not significantly affected by CO_2 or SO_2 treatment during pod filling stages. It is noteworthy that the reductions in CHL were of similar magnitude under the two CO_2 environments, suggesting that the PS results in response to SO_2 were likely not caused by differential reductions in CHL. The differential responses of SO_2 on PS rates under the two CO_2 environments may be explained by a delay in the senescence process caused by elevated CO_2, which would be most apparent during pod filling. Rudorff et al. [31] also observed that the CO_2 factor had no influence on PSII in wheat.

Our results failed to find a significant effect of elevated CO_2 on either dry matter yield or seed yield. This is very much against expectations for soybean which has been suggested to be one of the more responsive crops [2]. Prior and Rogers [27] showed a significant increase in yield under water stressed and well-watered conditions. The failure to find significant CO_2 responses for growth and grain characteristic, is likely owing to variability introduced by lodging in the CF+CO_2 treatments, especially during pod fill. This resulted in some of plants being covered by thick vegetation thereby producing smaller seeds. The LAI data were also disrupted during the pod fill stage by lodging of plants in the CO_2 enriched plots.

Recently, Tausz et al. [38] studied physiological responses of spruce trees to elevated CO_2 (0.8 mL L^{-1}) and SO_2 (0.06 μl L^{-1}) for three months. They also noted that all effects of SO_2 and CO_2 were independent of each other, i.e. significant $SO_2 \times CO_2$ interactions on gas exchange and biomass were not observed. Studies conducted on soybeans by Miller et al. [22] revealed that several cultivars apparently tolerated cumulative SO_2 dosages up to 0.10 μl L^{-1} with some showing beneficial effects at very low exposure concentrations. The 'Essex' cultivar used in the present study appears to exhibit SO_2 tolerance somewhat similar to that of NK 1492 used by Miller and colleagues (1979) [22]. The low level of SO_2 reported for Maryland during the summer monthly 24 hr average (0.006 μl L^{-1} SO_2) suggests that soybean cultivars having tolerance levels comparable to 'Essex' cultivar would likely not show significant losses in biomass yields in response to SO_2 air pollution; however, there could be some interactive effects between O_3 and SO_2 on soybeans as suggested by Heggestad et al.'s [14] earlier studies with the Essex cultivar.

5. Conclusion

Leaf PS, leaf DW (during pod fill), and LAI (during canopy development) were significantly increased under enriched CO_2. Total biomass and grain yields were not significantly affected by CO_2, which may relate to lodge of plants in high CO_2 plots. Plants grown under elevated SO_2 had decreased PS and LAI during pod fill stages, but nonsignificant trends for lower leaf characteristic, biomass and yields were found. Elevated CO_2 partially reduced the negative effects of SO_2 stress. The SO_2 treatment at ambient CO_2 conditions reduced LAI during canopy coverage but effects were not significant later in the growing season. Although the grain data failed to show significant effects of CO_2 and SO_2 treatments, the PS and LAI results during pod fill stages did support the hypothesis that elevated CO_2 partially inhibits the damaging effects from modest exposure to SO_2. Cultivar sensitivity to SO_2 may alter such support concerning $CO_2 \times SO_2$ interactions.

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